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FORM AND FUNCTION IN *TRISIDOS* (BIVALVIA) AND A COMPARISON WITH OTHER BURROWING ARCOIDS

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ABSTRACT

Trisidos Röding, 1798, is unique among the Arcoida in the marked twisting of the posterior portions of the shell around the hinge axis. Studies of live *T. yongei* Iredale, 1939, show that this twisted shell is adaptive for slow, shallow burrowing and byssal attachment in moderately physically rigorous sedimentary environments.

Analysis of the functional morphology of *Trisidos* and other modern arcoids suggests that arcoid burrowers may have evolved three distinct morphologic strategies as a compromise between burrowing efficiency and minimal resistance to ventilating currents at the shell margins and within the mantle cavity. Inflated shells with projecting umbos (e.g., *Anadara* and *Noetia*) allow for spacious lateral mantle cavities but offer minimal shell streamlining. Laterally compressed and subcircular shells (e.g., *Limopsis* and *Glycymeris*) are moderately streamlined and offer a wide margin for ventilating currents. The third morphologic strategy, represented only by *Trisidos,* combines streamlining of the shell anterior with posterior twisting, which again permits more efficient ventilation of the mantle cavity. Another adaptive advantage is conferred by this twisting and also by the anteroposteriorly compressed form of other burrowing arcoids. These features allow the slow-burrowing animals to more quickly achieve a "low-profile" life position and thus avoid adverse effects of current scour.

While preventing extreme specialization, the morphological limitations of arcoids have tended to preserve their evolutionary potential to make repeated transitions from infaunal to epifaunal life habits and back. The versatility of the pedal-byssal apparatus has probably played a role in this respect.

Data concerning hinge dentition and shell morphology suggest that *Trisidos* evolved from a morphologically less specialized representative of the Arcinae similar to the modern *Barbatia. Barbatia* was preadapted for the evolution of a shallow burrowing life habit because of its relatively efficient ligament and streamlined shape, features initially evolved as adaptations for epifaunal nestling.

INTRODUCTION

The bivalve order Arcoida is an ancient group within the subclass Pteriomorphia, whose fossil record dates back to early Paleozoic time. Arcoids are generally characterized by ecological conservatism, as evidenced by their never having evolved cementing, swimming, or even deeply burrowing forms. On the other hand, their numerous fossil and Recent species represent a number of distinct adaptations for "primitive" shallow burrowing, epifaunal or semi-infaunal nestling, and, in one instance (*Litharca*), hard substratum boring.

Perhaps none of the morphological adaptations developed by the Arcoida is more unusual and striking than the posterior shell twisting in the genus *Trisidos* Röding, 1798. In some species of *Trisidos* the posterior commissure plane has rotated in the course of evolution almost 90° relative to the shell anterior (Fig. 1). Despite the uniqueness of this shell form, its functional significance has not been fully analyzed.

In this paper we provide ecological observations on one of the more highly twisted of the *Trisidos* species (*T. yongei* Iredale, 1939) from Queensland, Australia, and using this information, attempt to interpret the evolution of this genus from a functional point of view. These observations of *Trisidos* and other burrowing arcoids provide new insights into the conservative nature of adaptive radiation within the ancient order Arcoida.

MATERIALS AND METHODS

Live *T. yongei* was dredged at depths of 2–4 m below the mean tidal level off the leeward (western) side of Magnetic Island, Queensland, Australia, in April of 1973. Magnetic Island lies within the Indo-Polynesian Province as delimited by Briggs (1974),

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and is situated between the Australian mainland and the Great Barrier Reef. The life habits of four individuals of *T. yongei* were observed on their native substratum. Ciliary current patterns and particle transport were observed by removing one shell valve and the corresponding mantle lobe, and then by introducing carmine or carborundum particles into the mantle cavity. Soft parts were studied from dissections of fresh material.

Additional data on shell form and habitat for other arcoids were obtained from a variety of literature sources, and from the collections at the Yale Peabody Museum (New Haven, Conn.), the National Museum of Natural History (Washington, D.C.), and the American Museum of Natural History (New York).

COMPARATIVE ANATOMY AND LIFE HABITS

Shell form

Although all fossil and Recent species of *Trisidos* are characterized by posterior shell twisting, this feature is particularly emphasized in the Australian species *T. yongei.* Especially striking here is the angularity of the posterior margin, which is set off from the more anterior parts of the shell by an umbonal to posteroventral angular deflection (Figs. 1 and 3a). In fossil species of *Trisidos,* e.g., *T. fajumensis* (Oppenheim, 1906), Eocene, Egypt; *T. yatsuoensis* Fujii, 1961, Miocene, Japan; *T. prototortuosum* Noetling, 1901, Tertiary, India), and in the Recent *T. tortuosa* (Linné, 1758), Indo-Pacific, the posterior twisting and angularity are less pronounced. As is evident from the localities listed here, modern and fossil *Trisidos* are restricted to the Indo-Pacific Region. Only one species, *T. tortuosa,* is represented by both Recent and fossil material (e.g., Tertiary of Mozambique, Moura, 1969).

Aside from its posterior twisting, *T. yongei* and other species of this genus are typically arcid in their shell form and hinge dentition.

Soft parts

The soft parts of *T. yongei* likewise resemble those of other modern arcids except for minor differences directly related to posterior twisting. For example, the left and right valve adductor muscle attachment scars in *T. yongei* are about equal in size, but only the left one is subquadrate in shape. Also correlated with twisting is an unusual elongation of the attachment surface of the left-valve posterior pedal retractor muscle.

These observations differ slightly from those by Ghosh (1924) for *T. tortuosa.* In this species, the left-valve adductor muscle attachment scar is triangular and smaller than in the right valve. Ghosh (1924) also noted that abdominal sense organs are absent in *T. tortuosa* and that esophagus and stomach are distinct. However, these two latter observations were subsequently contradicted by Heath (1941). Additionally, Heath mentions the following four general differences between *Trisidos* and most other arcoids: 1) the right abdominal sense organ is larger than the left; 2) the esophagus and stomach are difficult to distinguish; 3) the alimentary canal penetrates the heart; and 4) the labial palps show large, undulating folds in addition to the more typically arcoid smaller ridges.

In conclusion, except for the labial palp and alimentary canal features, most of the distinguishing anatomical features of *Trisidos* can be directly related to its evolution of shell twisting and the resulting inequivalve condition.

Mantle cavity currents and particle sorting

As in many burrowing arcoids, water for respiration and feeding enters the mantle cavity at the posteroventral shell margin through apertures formed by the local and temporary appression of the mantle lobes. This appression also defines a posterodorsal aperture for the exhalant current. Particles trapped by the gills are sorted, and either rejected by a posteriorly-directed gill ciliary tract, or accepted for further sorting and ingestion by anteriorly-directed ciliary feeding tracts. Particle rejection tracts are located on the mantle and foot as well as on the gills. These ciliary feeding and rejection tracts do not differ appreciably from the common arcoid pattern as developed in *Arca* and *Glycymeris* (Atkins, 1936), *Anadara* (Lim, 1966), *Noetia* and *Barbatia* (Tevesz, personal observations), *Limopsis,* and to some extent, *Philobrya* and *Lissarca* (Tevesz, 1977). Rejected particles are removed from the mantle cavity by being bound in mucus strings and ejected through the inhalant aperture by sudden valve contraction.

Life habits

Specimens of *T. yongei* were found living in a muddy, fine to medium sand substratum containing abundant fragmental shell material. The environment where the collections were made was subject to the effects of tidal currents and wave activity. Nevertheless, the area was protected on one side by the nearby mainland and on the other side by Magnetic Island and the more distant Great Barrier Reef, so the general environment in which *T. yongei* lived is properly termed moderately physically rigorous. This is somewhat similar to the environment inhabited by *T. tortuosa* (Ghosh, 1924). Ghosh cited a note from the Director of the Biological Station at Ennor (Madras, India) indicating that *T. tortuosa* "is fairly numerous in certain parts of Palk Bay between 4½ to 6½ fathom lines on a bottom of dirty muddy sand, and is not found in crevices." This information is important, since it confirms our observation that *Trisidos,* unlike other representatives of its subfamily Arcinae, is typically a burrower (rather than a nestler or rock-borer).

Specimens of *T. yongei* left in a laboratory tank on their native substratum for several hours showed an integrated burrowing activity consisting of the following sequence: 1. The foot emerges anteroventrally, probes the substratum, and anchors itself in the sediment. 2. Although initially lying with the anterior commissure plane more or less horizontal, *T. yongei* assumes a vertical orientation of this commissure plane as the anterior of the shell penetrates the substratum. Because the shell posterior is torted approximately 90° relative to the anterior, its posterior commissure plane therefore assumes a more or less horizontal position relative to the sediment-water interface. 3. A slow sequence of extension, expansion, and contraction of the foot pulls the shell diagonally downward into the substratum until the shell is shallowly buried with only the shell posterior exposed. The posterior commissure is then horizontal to and only a few millimeters above the sediment-water interface. Sequential positions of the shell during this burrowing sequence are illustrated in Fig. 1.

Once the animal is sufficiently buried in the substratum, it attaches to larger sediment particles (especially shell debris) by means of an exceptionally long byssus. The byssus fibers may attain a length of up to one half the length of the shell. This burrowing sequence may take several hours to complete, since it is commonly interrupted.

Because of the valve inequality and the horizontal position of the posterior shell margins, the longer, uppermost left valve forms a slightly projecting shelf above the shorter right valve. In terms of its semi-infaunal life habit, *Trisidos* is unique among modern representatives of the subfamily Arcinae. Other modern members of this subfamily are either epibyssate (*Arca* and *Barbatia*) or endolithic (*Litharca*: Frizzell, 1946). According to Thomas (1978), some fossil species of *Barbatia* were endobyssate.

MORPHOLOGICAL COMPARISONS WITH OTHER ARCOIDA

A number of arcoids are known to be burrowers or are inferred burrowers on the basis of their shell form. These include the modern Limopsidae and Glycymerididae (Limopsacea), certain Noetiidae and Anadariinae (Arcacea), and the largely fossil Cucullaeidae (Arcacea) (Stanley, 1970; Tevesz, 1977; personal observations). The family Cucullaeidae is represented by a single surviving genus, *Cucullaea,* which is almost certainly a shallow burrower, but whose life habits are otherwise little known. The presumed ancestral arcoid superfamily Cyrtodontacea and some Parallelondontidae (early Arcacea) are likewise inferred to have been burrowers (Pojeta, 1971; Stanley, 1972).

Modern arcoid burrowers naturally comprise three morphologic groups defined by lateral compression and umbonal projection. Group I burrowers show laterally inflated shells with strongly projecting umbos, as in *Anadara* and *Noetia* (Fig. 2a). Group II burrowers are laterally compressed, dorsoventrally expanded, and show relatively subdued umbos, as in *Limopsis* and *Glycymeris* (Fig. 2b). Group III burrowers are morphologically similar to the epifaunal nestler *Barbatia* and are intermediate in terms of lateral compression (in the shell anterior) and umbonal projection. Group III burrowers are represented only by *Trisidos.*

An interesting aspect of the form of these modern burrowing arcoids is that none of them have evolved a streamlined morphology, i.e., a form that is at the same time both laterally *and* dorsoventrally compressed. This is unusual because a streamlined form enhances burrowing efficiency (Stanley, 1970) and thus might confer survival-related advantages to these burrowing arcoids.

This lack of streamlining further documents observations made by Thomas (1976) regarding the morphological and ecological limitations of arcoids. Thomas cogently argued that the weak duplivincular ligament of most arcoids is a major cause of this conservatism.

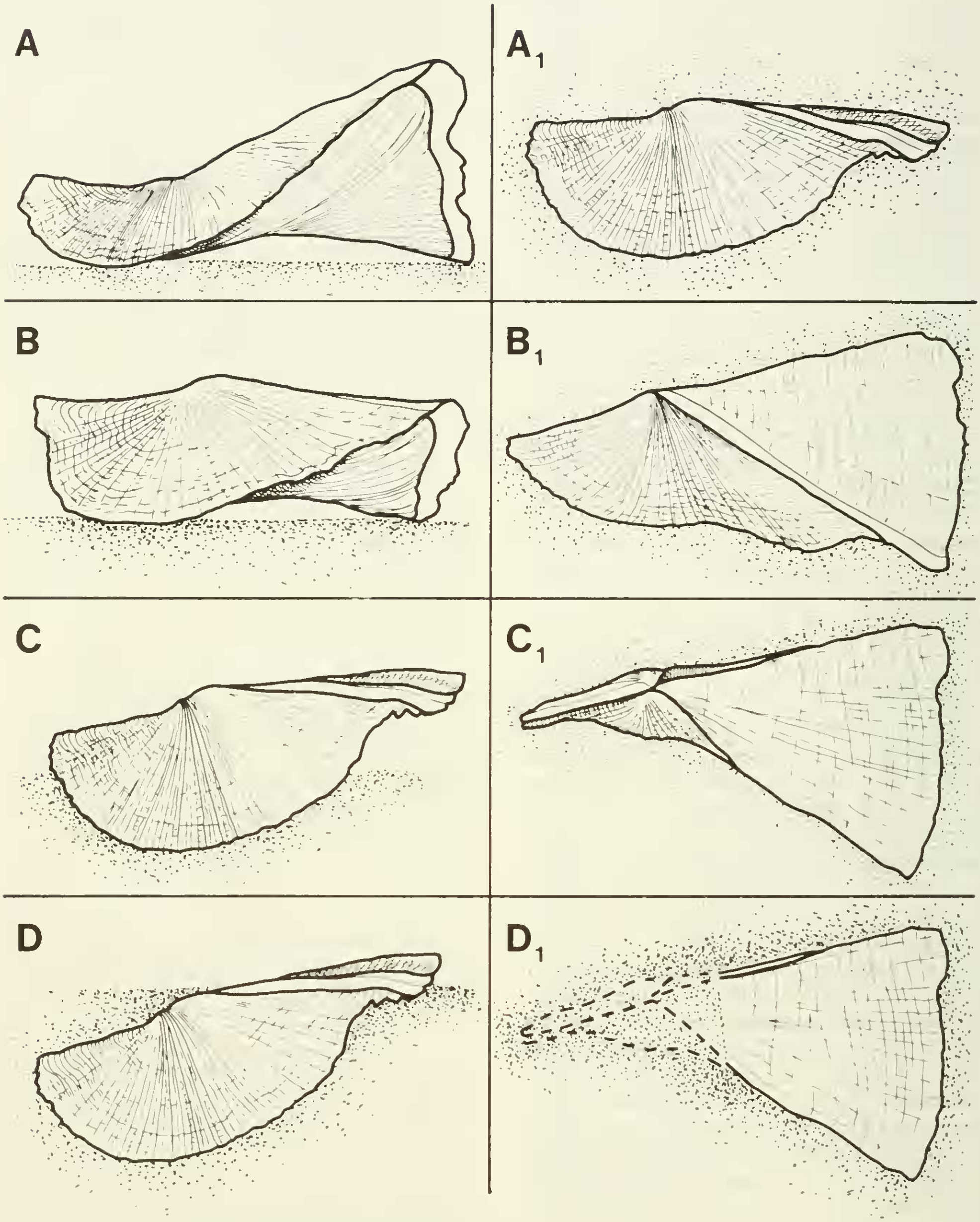

FIG. 1. Sequential shell orientations of live *Trisidos yongei* during burrowing. A–D = side view; A_1–D_1 = corresponding top view; A,A_1 = prior to burrowing; B,B_1 = burrowing; C,C_1 = burrowing; D,D_1 = usual life position.

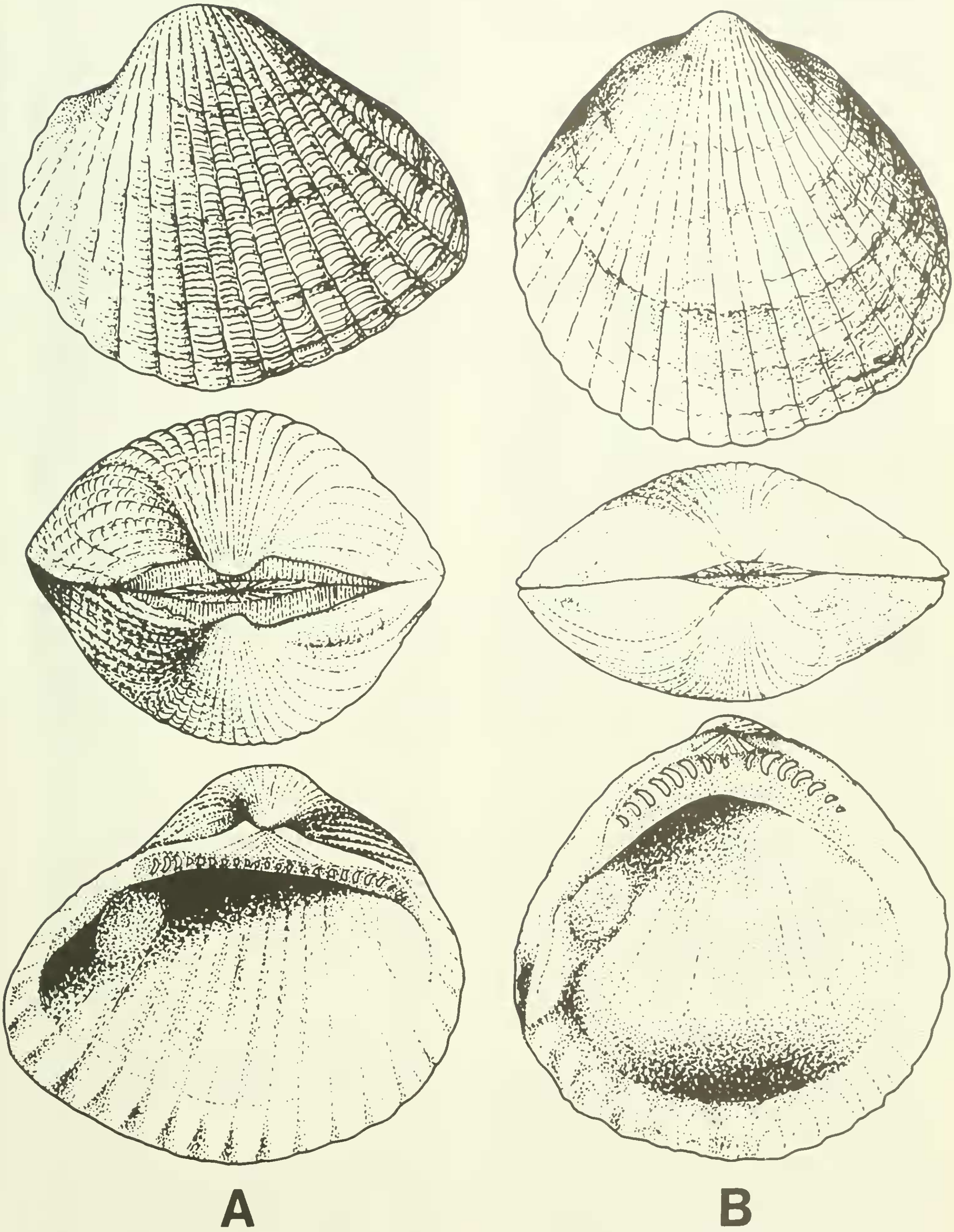

FIG. 2. Genera representing two morphologic groups of burrowing arcoids. Exterior and interior views of left valves and dorsal views of articulated valves for: A) *Anadara* (Group I); and B) *Glycymeris* (Group II). Respective actual lengths = 57 mm and 24 mm.

LIMITATIONS ON THE EVOLUTION OF SHELL FORM IN BURROWING ARCOIDS

Mantle cavity ventilation

We offer the working hypothesis that in addition to the ligament, factors relating to improving mantle cavity ventilation and minimizing frictional resistance of water currents within the mantle cavity may have influenced shell form in burrowing arcoids.

Group I forms typically live with the anterior portion of the shell buried in the substratum, so the substratum precludes freedom of circulation of an anteroventral inhalant mantle current. This current must therefore be restricted to the shell posterior, or at least to the posteroventral shell margin, thereby increasing frictional resistance at these mantle margins. Possibly to ease the resultant frictional resistance on the mantle currents, Group I burrowers have inflated their valves and increased the depth of their umbonal cavity. This significantly increases the volume of the lateral mantle cavities, thereby reducing the frictional resistance of their circulating water currents.

In contrast, Group II arcoids have partially streamlined their shells by increasing their lateral compression and by reducing the prominence of their umbos. But lateral compression decreases the volume of the lateral mantle cavities, thereby increasing frictional resistance on the interior mantle currents. Consequently, these species may have retained a non-streamlined sub-circular lateral profile in order to increase the area of anterior inhalant and anterior and posterior exhalant currents (see Atkins, 1936). Because Group II burrowers are commonly found in coarser sediments (such as gravels) than Group I burrowers, they can potentially utilize more of their mantle margins for mantle cavity ventilation, thereby not only reducing the frictional resistance of these currents entering the shell, but also likely promoting circulation within the mantle cavity.

Trisidos combines features of Group I and Group II burrowers. Its twisted form creates a lateral expansion of the mantle cavity in the posterior portion of the shell. Moreover, the posterior margin is expanded and elevated above the substratum (but at a low angle). This allows for spacious areas of mantle margin that are free from the substratum and which may be utilized for mantle cavity ventilation.

As noted previously, the ligamental hypothesis of Thomas (1976) adequately explains why arcoids have generally been unsuccessful in evolving active burrowers ecologically comparable to those in certain veneroid superfamilies. But this ligamental hypothesis fails to explain why arcoids have evolved and maintained throughout their long evolutionary history two major morphologic groups among their burrowing forms, neither of which is characterized by a totally streamlined shell form that would minimize, rather than aggravate, the limitation of their weak duplivincular ligament on burrowing efficiency. Nor does the ligamental hypothesis account for the fact that the one burrowing arcoid genus with total shell streamlining in its anterior, i.e., *Trisidos,* has not maintained this streamlined profile in its posterior. Because of the structure of duplivincular ligaments, maximum ligament efficiency is obtained in arcoids with a short interumbonal distance and, consequently, with strong lateral compression. Arcoids with a short interumbonal distance are capable of maintaining proportionally more ligamental lamellae attached between the two shell valves as the ligamental areas separate during shell growth. On the basis of considerations of burrowing efficiency, one might expect that burrowing arcoids would generally be dorsoventrally compressed for streamlining and laterally compressed for both streamlining and ligament strength, i.e., morphologically similar to certain epifaunal *Barbatia.*

This hypothesis makes no assumption regarding comparative pumping efficiencies of arcoid filibranch versus more complex veneroid eulamellibranch gills. The ventilation hypothesis assumes only that, in connection with the anatomy and burrowing habits peculiar to arcoids, relatively free access to mantle ventilating currents can be adaptively advantageous, and can therefore partially influence the shell morphology of arcoid burrowers. The possibility remains that eulamellibranch gills offer greater potential than filibranch gills for the evolution of mantle fusion, siphon formation, and deeper and more streamlined burrowers. But analysis of the evolutionary significance of gill type between arcoid and veneroid bivalves must take into consideration a wide range of variables, including efficiency of particle sorting, size and shape of the mantle cavity and gills, and possibly other factors in addition to pumping efficiency. Such comparisons between the Arcoida and Veneroida are beyond the scope of the present paper.

Stability in physically rigorous environments

Inasmuch as burrowing arcoids are typically limited in their burrowing rate and tend to occupy current-swept sediments (Thomas, 1975, 1976) their long exposure during reburrowing may be an additional factor influencing the evolution of posterior twisting in *Trisidos* and a highly compressed valve to valve profile in burrowers such as *Glycymeris*. Trueman (1966, 1968a, b) and Trueman et al. (1966) showed that bivalves with extensive mantle fusion can build up relatively high water pressures within the mantle cavity. This water, expelled as jets from the pedal aperture, aids the foot in burrowing by loosening underlying sediments. In bivalves lacking an extensively fused mantle, water jets are not used as effectively, and the burrowing rate is generally slower. Largely unfused mantle margins characterize the modern burrowing arcoids, and arcoids correspondingly require considerable time to assume their final infaunal life positions (i.e., with the posterior shell margin protruding only slightly, if at all, above the sediment surface; Stanley, 1968; 1970; Tevesz, personal observations). In this context, and especially because *Trisidos* is a slow burrower with an elongate shell in physically rigorous environments, its twisted posterior may be adaptive for reducing the hazard of current scour around the shell during burrowing as well as in its normal life position. Similarly, the compressed profile of *Glycymeris* results in reducing the exposure of the shell during burrowing, thereby minimizing current scour.

EVOLUTION OF *TRISIDOS*

As shown in Fig. 3, the epifaunal arcoid *Barbatia* is morphologically similar to *Trisidos* in terms of its lateral compression and moderately projecting umbos. These genera are likewise similar in their obliquely oriented hinge teeth, radial external ribbing, and in some *Trisidos* species, in their beaded external ornament. *Trisidos* differs from *Barbatia* primarily only in its twisted shell posterior, the absence of a prominent ventral gape (compared to some epifaunal *Barbatia*), and associated minor changes in internal anatomy (see above). Since *Barbatia* has a long fossil record prior to the Eocene appearance of *Trisidos* (Newell: N252–N254, in Cox et al., 1969), it is reasonable to assume that it is ancestral to *Trisidos*.

Epifaunal *Barbatia* might be considered preadapted for the evolution of a burrowing life habit because of its streamlined, wedge-shaped anterior and relatively subdued ornament. It may also be preadapted because its closely spaced umbos make possible a relatively strong duplivincular ligament (Thomas, 1976). A strong ligament would be

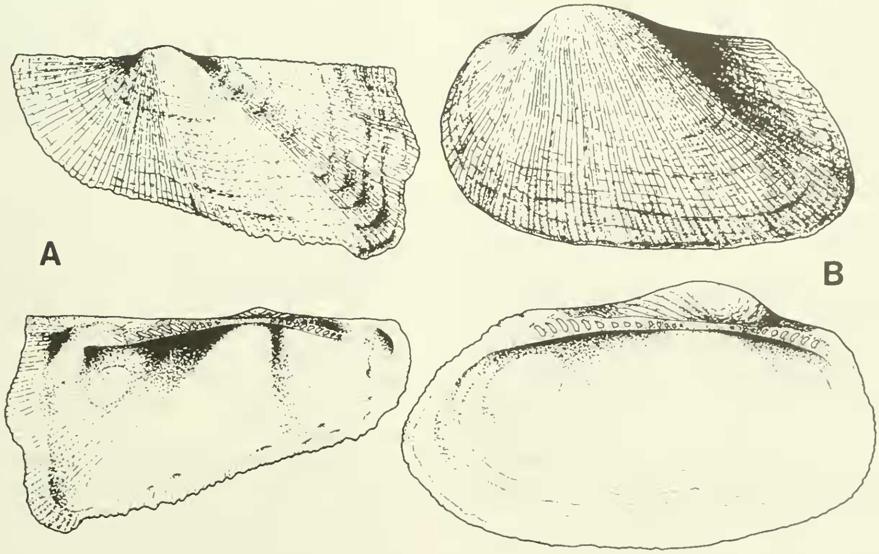

FIG. 3. Comparative shell features of *Trisidos* and *Barbatia*. Exterior and interior views of left valve for: A) *Trisidos yongei* Iredale. Australia. B) *Barbatia novaezelandiae* Smith. New Zealand. Respective actual lengths = 36 mm and 41 mm.

advantageous for pressing the shell valves against the burrow walls, especially in a species lacking fused mantle margins. Unlike the burrowing arcoids, *Barbatia* may have been able to evolve such shell streamlining because its epifaunal life habit imposes few restrictions on the area of its shell margin utilized for ventilating currents. As noted by Bretsky (1976), *Barbatia* utilizes its ventral shell margin for maintaining the inhalant mantle current, thereby leaving the entire posterior shell margin for the exhalant current. *Barbatia* is occasionally found nestling in cryptic habitats, but its inhalant area is still generally sufficiently elevated above the substratum to allow for free circulation of water currents. The laterally compressed form of *Barbatia* is clearly advantageous in connection with its habit of nestling in crevices, and its moderate dorsoventral compression is likewise advantageous for concealing the shell in this ecological setting.

But according to the ventilation hypothesis elaborated above, the evolution of infaunal burrowing in an arcoid with the shell morphology of *Barbatia* would be accompanied by problems of mantle cavity ventilation. Reduced ventilation may have resulted in connection with its laterally compressed mantle cavity when the ventilating currents became restricted to the posterior shell margins, i.e., above the sediment-water interface. In their evolution of burrowing life habits, the hypothesized descendants of *Barbatia* might have solved the mantle ventilation problem by evolving greater lateral inflation of the valves and a deeper umbonal cavity (as in *Anadara*), or by evolving a rounded lateral profile (as in *Glycymeris*). But these two alternatives require major remodeling of the shell. The ancestors of *Trisidos* evidently followed an evolutionary pathway involving greater economy of change, i.e. simple twisting in the shell posterior. This twisting was accomplished, as noted above, with minimal change in internal anatomy and with retention of both lateral and dorsoventral streamlining in the shell anterior. While increasing the area of the posterior shell margin elevated above the sediment-water interface and while increasing the internal volume of the posterior mantle cavity, the posterior twisting in *Trisidos* also improved the stability of the shell by creating a low profile in its living position.

It is interesting to speculate that the hypothesized change from epifaunal nesting to infaunal burrowing in the evolutionary history of *Trisidos* may have greatly influenced the nature and amount of suspended sediment entering its mantle cavity. In addition to bringing its inhalant area close to the sediment-water interface, the unique burrowing habit of *Trisidos* caused its inhalant and exhalant currents to lie in a similar position relative to a horizontal plane along the sediment surface. Consequently, these two currents may be less efficiently separated in *Trisidos* than in its hypothesized epifaunal ancestors.

SUMMARY AND CONCLUSIONS

As noted by Thomas (1976), the weak arcoid ligament has apparently limited evolutionary specialization by arcoids for both deep burrowing and permanent epibyssate attachment, because it limits valve gape in burrowing and anterior reduction. It is presently proposed that problems of mantle ventilation and shell stability in the context of slow burrowing have additionally imposed restrictions on the evolution of streamlined *shallow* burrowers in this order. But Thomas (1976) also noted that the inherent limitations on arcoid evolution have nevertheless permitted arcoids to make repeated transitions from epifaunal to infaunal modes of life and back. For example, according to Stanley (1972), the early Arcoida demonstrate a general evolutionary trend from ancestral burrowing to epifaunal life habits. Within the Arcacea, the Arcidae apparently evolved at an epifaunal grade of evolution and later reverted to the infaunal habit in many species. Later, certain infaunal Arcidae re-radiated back to the epifaunal habit, e.g., in the origin of *Arcopsis*. The infaunal Limopsidae (Limopsacea) likewise radiated into the epifaunal habit with the origin of the Philobryidae (Tevesz, 1977).

The invasion of a new adaptive zone is often accompanied by high-level taxonomic diversification (Simpson, 1953; Valentine, 1973). Arcoids exemplify this trend because their evolutionary life habit transitions are frequently accompanied by the appearance of new taxonomic categories, even at the superfamily level (Pojeta, 1971; Tevesz, 1977). In this respect, the ecologically versatile pedal apparatus of arcoids may have played a major role in their preadaptation for the evolution of both burrowers and epifaunal species. In addition to providing a powerful burrowing organ, it can afford firm byssal attachment in the epifaunal forms. The versatility of this pedal apparatus possibly compensated for their limitations in ligament strength, thereby allowing for their evolutionary persistence and for much of their ecological diversity.

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Note added in proof:

After this paper was accepted for publication, G. McGhee (*Lethaia*, 1978, 11: 315–329) published a paper concerning the theoretical implications of shell twisting in *Trisidos* and other bivalves. The reader is referred to this paper for this theoretical treatment.